Original Articles

Minnows may be more reproductively resilient to climatic variability than anticipated: Synthesis from a reproductive vulnerability assessment of Gangetic pool barbs (*Puntius sophore*)

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ABSTRACT

Information on various aspects of reproductive traits of female pool barbs from various stretches of Ganga River basin, India was generated in relation to climatic variability. The presumptions surrounding – minnows being the first and easily hit by climatic variability, was validated. GAM models revealed low threshold rainfall requirement (> 50 mm) within a wide temperature range (20–30 °C) necessary for attainment of breeding GSI (> 10.5 units). Pre-spawning fitness ($K_{spawn50}$) and size at 50% maturity (L_{M50}) benchmarked through Kaplan-Meier survival estimates were in the range 1.61–1.67 units (Fulton condition factor) and 8.6–9.0 cm respectively. Mapping of climate preferendum through LOESS smoothing hinted both low-mild rainfall (50–150 mm) and high rainfall conditions (400–700 mm) conducive for attaining pre-spawning fitness while no dependence on temperature was observed. First maturity of females was encountered at 4.7 cm within the size range 4.4–12.6 cm. The present study hinted a probable reduction (1.4–1.8 cm) in size at maturity of female pool barbs. We observed pool barbs can breed within a wide thermal regime following slightest of rainfall events. Collating this with the present rates of climatic variability, we infer negligible threat of changing climate on reproduction of *Puntius sophore* in near future – contrary to the existing presumptions. Owing to the easiness in attainment of pre-spawning fitness under an apparently flexible climate preferendum, 'skipped spawning' decisions while facing climatic variability also seem minimum. The recorded breeding thresholds may serve as future references while assessing climate driven changes on reproduction and evolutionary adaptations in Gangetic minnows.

1. Introduction

Small indigenous fishes (SIFs) fished from inland waters of India are perhaps the most ignored yet an indispensable component for inland fisheries – owing to its major contribution in diversity and its paramount importance as poor man's food fish. SIFs are defined as native fishes which grow maximum up to the size of 25–30 cm in mature or adult stage of their life cycle. Out of 765 native freshwater fish species documented from Indian inland waters, about 450 may be categorized as SIFs. Among them, about 23% are highly important as food and/or ornamental fish (Sarkar and Lakra, 2010). The importance of SIFs as

'nutrient-dense' cheap sources of protein is also well documented (Mohanty et al., 2011). In recent years, many small indigenous fishes of India have become threatened or endangered due to pollution, over exploitation, habitat destruction, water abstraction, siltation, channel fragmentation, diseases and introduction of exotic varieties (Lakra et al., 2010). Impact of climate change may have been the least investigated subject for SIFs, but sporadic reports are coming up regarding changes in SIFs population due to climatic variability. In a recent study by Naskar et al. (2017), regional pre-monsoonal precipitation pattern and storm surges was found to have implications on the SIFs population in Gangetic floodplain wetlands of India. Years with

lesser pre-monsoonal thunderstorms and rains collated with a decline in the SIFs catch in the following year. Overall, climate change has implications on inland fishes and fisheries; primarily through recruitment followed by range distribution, larval survivability and aquatic food web interactions (Myers et al., 2017). The present study focused on reproduction. A thorough review of some recent 'climate change-fish reproduction' themed literature revealed that climate change and its impact on reproductive biology of fishes have multiple dimensions. It includes changes in breeding phenology, skipped spawning, changes in size at first maturity (in most cases, reduction), changes in fecundity, earlier/late migration of adults or larvae in response to changing environmental cue. The environmental cues primarily include - warmer water temperature and delayed or earlier flow pulse (through precipitation or melting of snow). In addition, altered predator-prey dynamics (food chain) of the aquatic ecosystem also determines the survivability of eggs and larvae in the natural environment (Lynch et al., 2016; Myers et al., 2017; Whitney et al., 2016). In terms of fish species and area studied, the diadromous or oceanodromous marine fish species have been studied more frequently than the freshwater fishes for climate change impact assessment (Sparks et al., 2017). Furthermore, most of the existing studies on freshwater fishes are limited to temperate areas (Hovel et al., 2017).

The present study selected *Puntius sophore* (Hamilton, 1822) as a representative species of the SIFs group along middle and lower stretches of River Ganga, India. *P. sophore,* commonly known as 'pool barb' or 'spot-fin swamp barb' is a small cyprinid (minnow) inhabitant of rivers, streams and ponds. The species is surface-pelagic, shoaling and herbivore in nature. Their preferred breeding grounds are shallow marginal waters. Besides India, they are widely distributed in Pakistan, Nepal, Bangladesh, Myanmar, China, Bhutan and Afghanistan. The conservation status of pool barb being 'least concern' and low commercial importance have been among the main reasons of imparting 'lesser priority' on this species from conservation or climate change impact assessment studies; a scenario common for SIFs (Anon, 2016; BdFish, 2017; Froese and Pauly, 2017). However, Genus *Puntius* has got immense significance with respect to biodiversity and taxonomy and several new species have been discovered in India (Pethiyagoda et al., 2012). Most of the studies on *P. sophore* till date have been on morphometrics, growth pattern, food-feeding habit and traditional reproductive biology studies, reviewed in Gupta (2015). Additionally, some studies have also been conducted on its nutrient composition (Mahanty et al., 2014), thermal tolerance (Mahanty et al., 2017), phylogeography (Negi et al., 2017) and genomics (Lakra and Goswami, 2011). Among regional fisher community and fisheries researchers, there exists a general presumption – 'minnows being the first and easily hit by climatic variability' or 'climate change has negative impact on SIFs population', without any formal data driven assessment (Sarkar et al., 2018a; Naskar et al., 2017; Mandal and Nandi, 2015; ICSF, 2010). In attempt to validate these 'presumptions', we assessed the reproductive vulnerability of a 'representative' minnow (vis-à-vis SIF) to changing climate. In our present attempt - we integrated all the indices, applied on a single species (environmental thresholds in Sarkar et al., 2018; pre-spawning fitness in Sarkar et al., 2017) and finally collated with climate data or historical reports on breeding season. This is the first such attempt on any minnow population or SIFs *per se*. Traditional fish reproductive biology studies generally include gonado-somatic index (GSI), breeding season, egg parameters and length at maturity. The importance of investigating environmental influences on gonadal maturation and spawning is also known in conservation themed research. However, the identification of natural breeding cue(s) and quantification of hydro-climatological thresholds for successful natural recruitment (breeding) in fishes is more of a recent area (Sarkar et al., 2017, 2018; Karnatak et al., 2018).

To assess the reproductive vulnerability of any fish species to climate change, availability of long-term data on reproductive indices is regarded as an 'asset'. Long term, precisely synchronized data both on reproductive indices and climatic variables are required for any formal quantitative assessment. By long term data – we mean time series data on reproductive traits pertaining to a species that come from common/ identical habitats. In developing countries like India, there is dearth of such long-term databases especially on inland fishes and fisheries (Sarkar and Lakra, 2010, Naskar et al., 2017). On an optimistic note – even if published reports are consulted, either the species/location does not match, or the reported observations appear fragmented/incomplete/pooled. Under these circumstances, our present approach may prove to be a viable alternative. We assumed – if the reproductive pattern of a species is screened long enough (two years in our case) over a continuous but wide geographical range (multiple stretches along River Ganga), the information generated is representative of the 'contemporary' breeding behavior. Such representative information is good enough to be collated with regional climate variability data. This way we get to understand the probable patterns in reproductive adaptation while facing specific trends of climatic variability. Based on these patterns, we can also forecast future adaptations in a scenario where present rates of climatic variability persists. Furthermore, repetitive or time series estimation of breeding thresholds for prioritized fishes may itself create a 'valuable database' for future fishery policymakers and climate researchers (discussed later). We coined the approach as *the four-step framework*. Similar novel approaches were developed to assess and/or forecast suspended sediments (Alizadeh et al., 2017; Chen and Chau, 2016; Olyaie et al., 2015) or water quality (Wang et al., 2014, Wu and Chau, 2006) in inland open waters; some recent examples. The viability of any novel approach (idea) in the field of environmental sustainability is evidenced to be largely dependent on the diffusion processes that facilitates acceptance and adoption; otherwise remaining futile (Aldieri and Vinci 2017).

The present study envisaged to quantify natural thresholds associated with successful recruitment of *P. sophore in-situ* using some new approaches. Number of 'breeding thresholds' were quantified; categorized into – 'biological' and 'environmental' thresholds. Biological thresholds include threshold GSI, pre-spawning fitness and sizes at maturity. Environmental thresholds imply the optimum concentration/ intensity of environmental cue at which some biological thresholds are attained to facilitate breeding. The objectives included – (a) to identify climato-hydrological influences on reproduction of *P. sophore* from River Ganga, India; (b) to quantify threshold GSI and breeding cues (environmental thresholds); (c) to benchmark threshold fitness (condition factor) for spawning; (d) to identify thermal and precipitation windows for attainment of pre-spawning fitness; (e) tracking changes in breeding phenology with regional climatic trends; (f) to assess the likely impacts of changing climate along Ganga River basin. Other biological thresholds like sizes at maturity (first maturity and size at 50% maturity) were quantified and compared with old records to explore possibility of any changes caused by natural selection over time under changing climatic scenario.

2. Materials and methods

2.1. Study area and species selected for study

Three sampling stations on river Ganga were selected: middle stretch *i.e.* Patna (25.6166 °N and 85.1989 °E), anterior lower stretch *i.e.* Farakka (24.7999 °N and 87.9158 °E) and posterior lower stretch *i.e.* Triveni (22.9844 °N and 88.4039 °E) (Fig. S1). One minnow species, *P. sophore* (Hamilton, 1822) commonly known as 'pool barb' or '*jat-punti*' (in vernacular language) was purposively selected as a representative of SIFs due to its consistent availability, heavy dependency by fisherfolk community and aquaculture (subsistence) importance. The species has a low market price throughout the year (around INR 100–200/kg or USD 1.5–3.1/kg) and consistently high daily-catch contribution (non-quantified – Anon, 2016).

2.2. Sample collection and analysis

On monthly basis, thirty specimens were collected from each stretch studied. Altogether 1237 specimens (423 female, 814 male and non-sexed) were collected between April 2015 and January 2017, spanning two breeding seasons. Only females were selected as model sex owing to the ease in observing gonadal maturity status. Fishes were collected using gill net, cast net, scoop net and seines during early morning (6:00–8:00) involving local fishermen. The nets had variable mesh size (5–20 mm) for collection of heterogeneous size groups. After collection, morphological measurements were taken. Specimen were dissected, ovaries carefully removed, weighed and preserved in 70% ethanol. Five commonly identifiable maturity stages were considered according to colour, texture, appearance, relative size of gonads and oocyte diameter: stage I – immature, stage II – maturing, stage III – mature, stage IV – ripe and stage V – spent (Alam et al., 2014, Qasim, 1973, Qasim and Qayyum, 1961). Descriptive data on female pool barbs sampled during the present study is furnished in Table S1.

Simultaneously with fish sampling, hydrological parameters were recorded following standard methodologies (APHA, 2005). The parameters recorded were: water temperature, dissolved oxygen (DO), free carbon dioxide, pH, total dissolved solids (TDS), conductivity, alkalinity (total), salinity, nitrate (NO_3^-) and phosphate (PO_4^-). Water samples were collected in duplicate *viz.* at the fishing site and away from the fishing site. For laboratory analysis, a composite water sample was prepared from the duplicate sub-samples (Gomez and Gomez, 1984). A fixed sampling time (7:00–8:30 am) was consistently maintained throughout the sampling period (preferably in the 2nd week of each month) for all the stations. Location-wise data on monthly rainfall (mm) was procured from Indian Meteorological Department (IMD, Alipore, West Bengal). Time series data (1980–2015) on mean air temperature, seasonal rainfall and total annual rainfall were also collected for each location to quantify long term climatic variability. Habitat parameters recorded during the study period are provided in Table S2.

2.3. Modeling climato-hydrological influence on GSI and threshold GSI for breeding

Firstly, pairwise correlation among environmental parameters was examined to diagnose multicollinearity. We adopted variance inflation factor (VIF) analysis to select environmental variables that were further plugged into the multiple linear regressions. Environmental parameters with VIF values < 10 were filtered out and selected for the next step (Marquardt, 1970). Secondly, the significant breeding cues were mapped through multiple linear regression; filtered environmental parameters as 'independent variables' and GSI as the 'response variable'. The 'place effect' was also incorporated into the model for examining spatial differences (if any) and to obtain estimates/trends that would be 'true' irrespective of spatial differences. The multiple linear regression was performed under the analysis of covariance (ANCOVA) framework. Thirdly, the relative importance of significant environmental parameters vis-à-vis breeding cues was determined through t^2 value. They were ranked in descending order of importance. Their nature of influence on gonad maturity (positive or negative) and threshold values for breeding was assessed from 'GSI vs. parameter' GAM (Generalized Additive Models) (Hastie and Tibshirani, 1986).

Fourthly, threshold GSI for onset of spawning (breeding GSI) was estimated by GAM using binary codes (1 = Mature, Ripe and 0 = Immature, Maturing, Spent) as response variable and GSI as explanatory variable. The rationale behind 'spent' stage not coded as '1' was to avoid dampening of threshold GSI values. The binary coded parameter was conceptualized as 'Breeding event'. Place effect was also incorporated here to eliminate the spatial differences while predicting threshold breeding GSI. Lastly, the breeding GSI value was used as reference GSI while identifying thresholds of environmental cues for

breeding. All analyses were done in 'R-software' (R Core Team, 2015). Clarifications on the choice of statistical methods can be found in the online Supplementary material (supplementary text).

2.4. Condition factor and egg parameters

Fulton's condition factor (K_F), hereinafter referred as *fitness*, was calculated using the formula given by Fulton (1904) as $K_F = 100 \times$ (W/L^3), where W is the body weight in g; and L is the total length in cm. The factor 100 is used to bring K_F close to unity (Froese, 2006). Range of egg parameters *viz.* total fecundity, egg weight and egg diameter at the pre-spawning stage were estimated from the preserved ovaries of mature and ripe females (*i.e.* fishes coded as 1 for modeling purpose, see above).

2.5. Pre-spawning fitness and identification of climate preferendum

Firstly, pre-spawning fitness ($K_{spawn50}$) was estimated using non-parametric Kaplan-Meier method for survival analysis (Kaplan and Meier, 1958). Lastly, thermal and precipitation window(s) for attainment of $K_{spawn50}$ (termed as climate preferendum) was identified using LOESS smoothing technique (Cleveland et al., 1992); climatic factors (temperature, rainfall) taken as independent variable and condition factor as dependent variable. LOESS (locally weighted scatterplot smoother) plots were visually inspected for identifying optima and/or trend. Fishes (females) in 'mature' and 'ripe' stage was coded as '1' while the rest coded '0'. All analyses were done in 'R' (R Core Team, 2015). Clarification on the choice of statistical method can be found in the online Supplementary material (Supplementary text).

2.6. Sizes at maturity

The total body length of the smallest mature fish (mature/ ripe) encountered was considered as first maturity size; a gross estimation of size at first maturity (Ainsley et al., 2011). Size at 50% maturity (L_{M50}) was also estimated using total body length data (binary coded like $K_{spawn50}$) of individuals through Kaplan-Meier estimate.

2.7. Climate data analysis

To study the climatic change in the study area, a standard '30-years normal' data analysis procedure was used. Daily mean air temperature and precipitation data of 30 years from 1980 to 2015 was obtained from IMD. The data corresponding to the grid of study location was extracted by using 'Raster package' in 'R' (R Core Team, 2015). Subsequently monthly time series means of air temperature and rainfall was computed from the extracted daily time series data. Finally, annual mean of mean air temperature and total annual rainfall were computed from monthly means. A simple linear trend analysis was carried out to find out the long-term trend. Subsequently, total rainfall during pre-monsoon, monsoon and post-monsoon were used to quantify changes in seasonal rainfall composition (Karnatak et al., 2018).

3. Results

3.1. Breeding phenology

Puntius sophore seem to have an extended breeding season at lower stretch of River Ganga (Farakka and Triveni). At Triveni breeding commenced from February and lasted till September (8 months in total). At Farakka, the species seem to breed between March-September (7 months). Although the Triveni stock appears to breed with a peaked GSI through February-September but in Farakka stock peak breeding occurs during April to July. Interestingly, few mature-ripe females were encountered during October-November at Triveni (posterior lower stretch) but not in Farakka (anterior lower stretch); hinting a probable
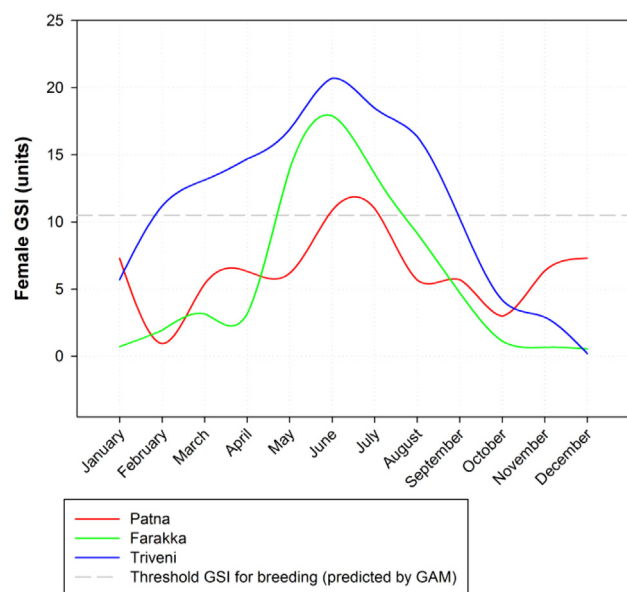
Fig. 1. Annual trend of female GSI of *P. sophore* along various stretches of river Ganga.

region-specific extended part. Such occurrences of mature-ripe females during autumn-winter months (October-November) have not been reported previously.

The duration of breeding phenology in the middle stretch (Patna) is nearly half of what exists at the lower stretches (Triveni and Farakka). In Patna, fish breeds within a strict monsoon calendar *i.e.* May to September (5 months) with peak spawning during June-July. Interestingly, a second but minor burst of gonadal activity was observed during winter months *i.e.* November-January where few maturing-mature females were encountered (Fig. 1). This has also never been reported before. Some information on breeding phenology of pool barbs from Indian waters already exists (Table 1).

3.2. Multicollinearity diagnostics and selection of environmental parameters

Multicollinearity has been detected among some environmental parameters. This is clearly visible in the pair-wise Pearson's (2-tailed) correlation plot generated in 'R-software' (Fig. S2). For example, high degree of correlation exists between TDS and Salinity, Conductivity and Salinity. Negative correlation exists between rainfall and other environmental variables such as DO, pH, Alkalinity, conductivity, TDS, Salinity etc. This implies that only few parameters are 'controlling factors' that can sufficiently explain the variability in the environmental conditions. Parameters with VIF values greater than 10 denote high degree of multicollinearity and were subsequently discarded. Parameters with VIF < 10 *viz.* water temperature, rainfall, dissolved

Table 1
Published information on breeding phenology of *Puntius sophore* from Indian waters (*arranged directionally from Northern to Southern parts of India*).

S. No.	Location	Breeding season	Reference
1.	Jammu and Kashmir	June-August	Langer et al. (2013)
2.	Tripura	June-September	Choudhury et al. (2015)
3.	Assam	June-August	Phukon and Biswas (2012)
4.	Uttar Pradesh	July-September[*]	Srivastava (2003)
5.	West Bengal	February-September[*]	Mitra et al. (2005)
6.	Andhra Pradesh	June-September	Reddy and Rao (1992)

[*] Selected for comparison with the present study. Mitra et al. (2005) for lower stretch and Srivastava (2003) for middle stretch of River Ganga.

oxygen, free carbon dioxide, pH, alkalinity, nitrate and phosphate (8 parameters out of 11) were selected for further development of multiple linear regression model (Table S3).

3.3. Climato-hydrological influence and threshold GSI for breeding

The multiple linear regression model with place effect taken into account had revealed that rainfall (t^2 *value: 42.42*) followed by water temperature (t^2 *value: 29.68*) > alkalinity (t^2 *value: 26.5*) > free carbon dioxide (t^2 *value: 21.64*) > phosphate (t^2 *value: 16.21*) > pH (t^2 *value: 7.04*) have crucial influence on gonadal maturity and breeding (*Multiple R-squared: 0.42; p-value: < 0.01*). Parameter wise – water temperature, rainfall and alkalinity have significant ($p < 0.01$) positive influence on GSI. Free CO_2, pH and phosphate had significant ($p < 0.01$) negative relationship with GSI. ANCOVA revealed that the environmental influence on breeding (*i.e.* influence on GSI) was significantly different ($p < 0.01$) in Patna stock from Triveni-Farakka stock. In nutshell, 'Patna stock' can be visualized as one group and 'Triveni-Farakka stock' as another group. This also partly explains the spatial differences in breeding phenology of the species in Patna (middle stretch) from that of Farakka and Triveni stocks (lower stretch), presented in previous section.

GAM model for threshold breeding GSI (Fig. 3) revealed that, irrespective of spatial differences, females having GSI ≥ 10.5 units can be considered ready for spawning (Breeding event = 1) (*R²: 0.88; Deviance explained: 88.2%; Generalized cross validation score (GCV): 0.03*). It was contemplated from the graph function that arrived at event 'one' (breeding) from 'zero' (no breeding) and thereafter attenuated a plateau. The GSI values of 'Patna stock' was found to be significantly different ($p < 0.01$) from 'Farakka-Triveni stock', remained low for most part of the year at Patna (Fig. 1).

Visual interpretation of 'environmental parameter-GSI' GAMs (Fig. 2) against threshold breeding GSI value (10.5 units) helped in quantification of breeding cues. GAM model revealed rainfall > 50 mm (*R²: 0.53; Deviance explained: 54.5%; GCV: 18.69*) as threshold rainfall for breeding. The dip in the model between 400 and 800 mm rainfall marks was due to lack of data support in this range, as evident from the wide prediction belt (low confidence). In terms of water temperature, no threshold could be predicted as such due to demonstrated instability in the graph pattern. A closer look on the model revealed that both low (around 20 °C) and high temperatures (> 30 °C) were conducive for optimal gonad maturation and probably breeding too; suggesting a wide water temperature cue between 20 and 30 °C (*R²: 0.36; Deviance explained: 37.4%; GCV: 25.71*). Waters with free carbon dioxide between 6 and 9 ppm (*R²: 0.37; Deviance explained: 38.9%; GCV: 25.09*), pH < 8 units (*R²: 0.35; Deviance explained: 36.6%; GCV: 26.03*), alkalinity between 40 and 80 ppm (*R²: 0.27; Deviance explained: 28.1%; GCV: 28.96*) and phosphate > 0.07 ppm (*R²: 0.41; Deviance explained: 42.8%; GCV: 23.51*) can be regarded as optimum for breeding, irrespective of spatial differences.

3.4. Pre-spawning fitness and climate preferendum

The pre-spawning fitness ($K_{spawn50}$) of female pool barb with 95% confidence interval (C.I.) was estimated at 1.63 ± 0.04 units (Fig. 4). The threshold condition factor (fitness) beyond which more than 50% of the population may attain readiness for spawning is indicated by the red horizontal line in the graph; coined as $K_{spawn50}$. Dotted lines represent 95% C.I. The average egg diameter, egg weight and absolute fecundity at this stage ranged between 0.54 and 0.62 mm (mean 0.59 ± 0.01 mm), 0.15–0.47 mg (mean 0.25 ± 0.01 mg) and 1187–30820 eggs (mean 5256 ± 516 eggs) respectively. In our dataset, the recorded K values ranged within 0.75–2 units.

The climate preferendum for attainment of pre-spawning fitness have been identified through LOESS plots where dotted lines represent estimated $K_{spawn50}$. No temperature window could be identified for
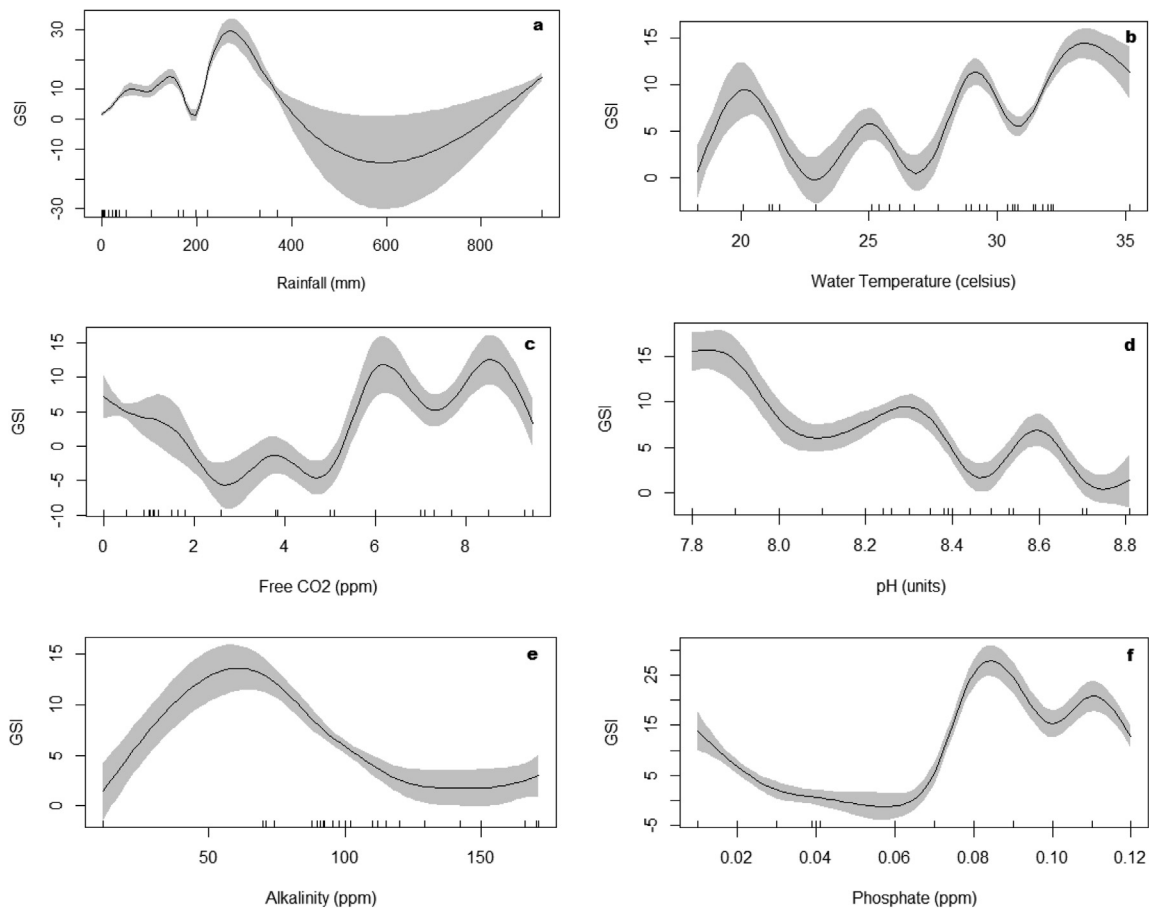
Fig. 2. (a-f): GAM models showing threshold values of key environmental parameters for breeding of *P. sophore*.
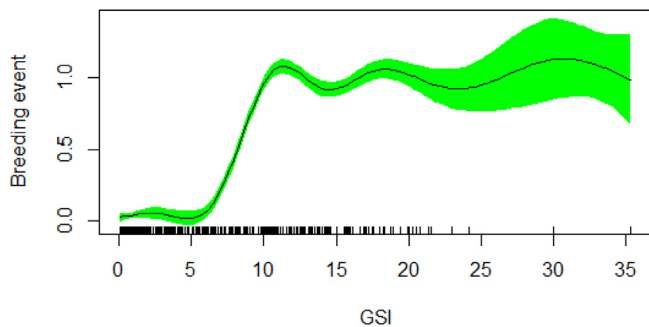

Fig. 3. GAM model showing threshold GSI for breeding of female *Puntius sophore* in River Ganga. Black dashes on the x-axis indicate data points.
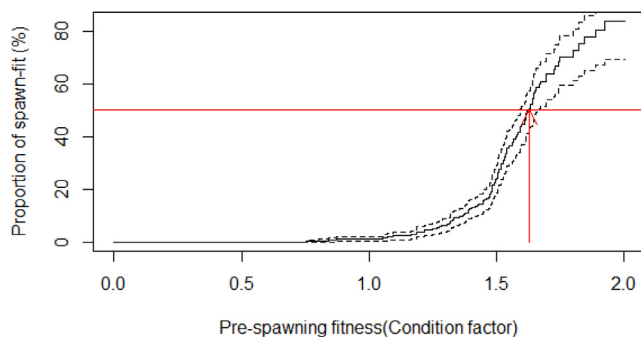

Fig. 4. Pre-spawning fitness ($K_{spawn50}$) of female *P. sophore* in River Ganga.

attainment of $K_{spawn50}$ due to under-fitted nature of the thermal pre-ferendum model ($r = -0.044, p > 0.05$) and a flatter trajectory of the 'water temperature-condition factor' function (Fig. 5a). The under-fitted nature of thermal preferendum model may have two reasons. Firstly, there may be negligible dependency on water temperature for attainment of $K_{spawn50}$. Lastly, the ability of pool barbs to breed over an extended period of the year (Fig. 1) across a wide thermal regime; body fitness levels synchronized accordingly. This partly explains en-countering of few mature-ripe females in autumn-winter months (Oc-tober-November) at Triveni and the winter-time burst in GSI at Patna. However, extrapolated interpretation of the model hints that the spe-cies can consistently maintain its fitness near $K_{spawn50}$ across a wide temperature range (15–35 °C). On the other hand, both low-mild rain-fall (50–150 mm) and high rainfall (400–700 mm) events seem op-timum for the attainment of $K_{spawn50}$ (Fig. 5b). The precipitation pre-ferendum model is under-fitted too ($r = 0.1, p < 0.05$) comparatively less than the thermal preferendum. The dip observed between 200 and 400 mm monthly rainfall may be due to successful spawning event (release of eggs) after attainment of pre-spawning fitness, resulting in overall dampening of condition factor values in sample (Fig. 5b). Re-emergence of precipitation preferenda curve beyond 400 mm monthly rainfall mark maybe due to lack of data support in this range. Only the former precipitation window (50–150 mm) has been considered for further discussions.

3.5. Size at maturity

First maturity was encountered at 4.7 cm within the size range of 4.4–12.6 cm. The L_{M50} *i.e.* total body length beyond which there is ≥50% chance of encountering a mature female, was estimated at
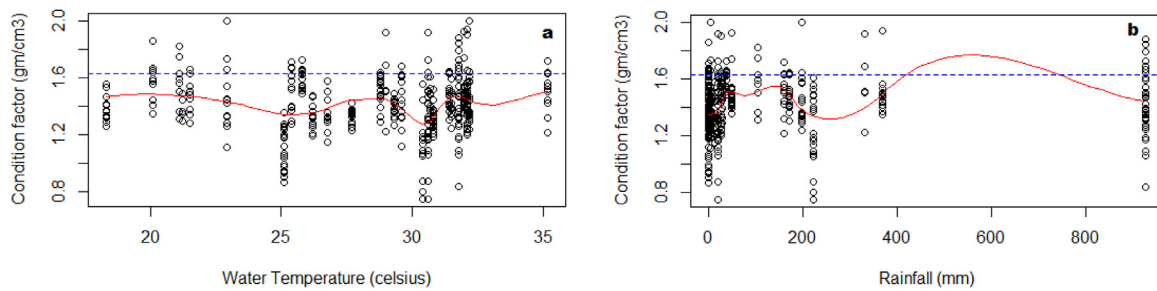
Fig. 5. (a, b): Climate preferendum (thermal-precipitation window) for attainment of $K_{spawn50}$ in *Puntius sophore*.
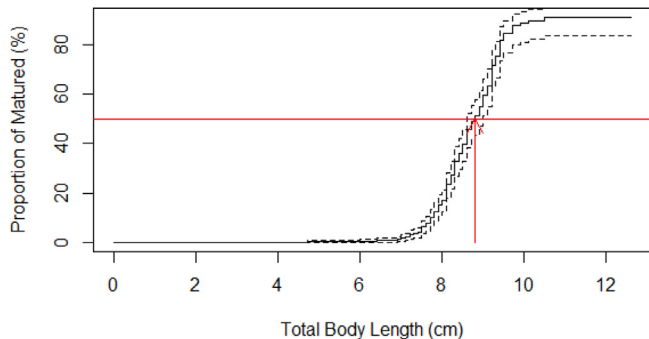

Fig. 6. Size at 50% maturity (L_{M50}) of female *P. sophore* in River Ganga.

8.8 ± 0.2 cm with 95% C.I. (Fig. 6). The minimum and maximum total body length encountered was 4.4 cm (at Triveni) and 12.6 cm (at Patna), respectively.

3.6. Trend of climatic variability over studied stretches

Analyses of the IMD data (1980–2015) on annual mean air temperature revealed a warming climate throughout the studied stretches of River Ganga, although spatial differences exist (Patna + 0.47 °C, Farakka + 0.36 °C and Triveni + 0.20 °C). The present trends are in conformity with Rathore et al. (2013). The total annual rainfall (1980–2015) has decreased by 307 mm at Patna, 580 mm at Farakka and 257 mm at Triveni. Seasonwise – the monsoon rainfall (May-August) in the middle stretch (Patna) has decreased by 4.2% while it increased during pre-monsoon (January-April, + 0.2%) and post-monsoon (September-December, + 4%). At the lower stretch, increase in monsoonal rainfall has been observed (Farakka + 3.8%; Triveni + 6.2%) while both pre-monsoonal (Farakka − 0.6%, Triveni − 2.4%) and post-monsoonal rainfall (Farakka − 3.3%, Triveni − 5.8%) has decreased. The present observations on changing precipitation pattern are in line with earlier observations (Kumar and Jain, 2011; Paul and Birthal, 2015).

4. Discussions

4.1. Importance of quantifying natural breeding thresholds in climate research

For better understanding of population-environment interactions, quantification of environmental and biological thresholds for breeding/spawning in fishes is important (Sarkar et al., 2017). Each fish species has its range of breeding thresholds which it may try to avail even in a changing climatic scenario (Crozier and Hutchings, 2014). In a changed climatic scenario, the time frame for availability of the environmental breeding thresholds in aquatic ecosystems may permanently shift, prolong or even narrowed (Crozier and Hutchings, 2014; Whitney et al., 2016). Fishes with wider breeding thresholds may likely have higher probability of successful adaptation and survival – more climate change

resilient. Likewise, fishes with narrower breeding thresholds may be less climate resilient. In absence of long term data, one can first explore the cascading effects of regional climatic variability (thermal-precipitation regime) on breeding cue(s) and then superimpose the simulated ecosystem scenario over the breeding thresholds data already quantified. This may hint to what extent the reproduction in a species will be changed, compromised or favored in future (Karnatak et al., 2018; Sarkar et al., 2017, 2018). In this light, we inferred Gangetic pool barbs as a reproductively resilient species under changing climate – contrary to the perceptions which anticipate otherwise (clarified below).

4.2. Breeding phenology

Some information on breeding phenology of pool barbs from Indian waters already exists, presented in Table 1. Although spatial variation in breeding phenology of pool barbs is demonstrated, temporal variations in breeding phenology is hard to assess for the species. This is due to the absence of any 'follow-up' or 'repetitive' studies on reproduction of *P. sophore* from the same or nearby area(s) to enable any comparison. The observed breeding phenology at lower Gangetic stretches (Triveni, Farakka) was compared with an earlier report by Mitra et al. (2005). On a comparative note, the present study recorded similar onset (February) but a stretched offset (from August to September) of breeding at the posterior lower stretch of River Ganga. A one-month shifting in breeding calendar from 'February-August' (Mitra et al., 2005) to 'March-September' was evident in the anterior lower stretch. This one-month extension or shifting in breeding phenology does not seem plausible enough to conclude any reproductive adaptation by the species. However, the presence of mature-ripe individuals during October-November at Triveni raises suspicion on the possibility of a region-specific extension of breeding phenology at the posterior lower stretch of River Ganga. This hypothesis, worth validating in future, seems realistic following observations by Negi et al. (2017); high genetic diversity among stocks of *P. sophore* in Indian rivers due to divergent distribution and development of localized breeding stocks (Negi et al., 2017).

In the middle stretch (Patna), no published information on breeding periodicity from the same (or nearby) areas exists. The only closest record available (252 km from Patna) is from Allahabad-Varanasi zone *i.e.* anterior middle stretch of River Ganga (Srivastava, 2003). Srivastava (2003) reported breeding season of *P. sophore* during July-September with peak at July-August. On a comparative note, the reported offset of breeding (September) matches with present observation. However, there appears an earlier onset of breeding (from July, presently to May) and extended duration (2 months) of breeding season. The peak spawning also appears to have advanced by one month *i.e.* from 'July-August' (Srivastava, 2003) to 'June-July' (present study). This two-month advancement-cum-extension of breeding phenology cannot be ignored and reflects reproductive adaptation in the species. Lastly, the presence of a minor winter-time burst in GSI (November-January) and few maturing-mature females hints a probable 'extended winter-breeding phase'; not reported previously. We could

not conclude a second breeding phase because the contribution of maturing-mature females during winter (November-January) was negligible and no spent or ripe females were encountered as such. This leaves scope for future validation.

4.3. Climato-hydrological influence and threshold GSI for breeding

The appearance of water quality parameters (e.g. free carbon dioxide, pH, alkalinity and phosphate) as 'breeding cues' may be due to spurious correlations resulting from mechanisms of increased rainfall, higher concentrations during periods of increased water temperatures vis-à-vis higher rate of evaporation and/or allochthonous nutrient inputs. Rainfall and water temperature were also observed to have correlation with the water quality parameters. In this light we assumed, water temperature and/or rainfall as the primary driver(s) having cascading effects on fish habitat quality. Although sudden changes in water quality parameters is known to trigger maturation and/or spawning in fishes, the triggering supposedly happens only after some thresholds of primary drivers (water temperature, precipitation, photoperiod, etc.) are satisfied (Sarkar et al., 2018; Karnatak et al., 2018). In tropical open waters like River Ganga, the perception of seasonality in habitat is mainly caused by changes in rainfall regime – not temperature as in temperate waters (Karnatak et al., 2018). Delineating environmental control on reproduction is difficult to probe *in-situ* without controlled experiments. The complexity is further aggravated for tropical fishes and open waters (Sarkar et al., 2018; Lam, 1983; Whitney et al., 2016). Therefore, our interpretation of results is largely emphasized on water temperature and rainfall for easier understanding of species response.

Information on climato-hydrological influences on gonadal maturity and breeding of *P. sophore* is absent; present study generated baseline information. It was found that changes in rainfall pattern may have the most profound effect on gonad maturation and spawning followed by the effect warming climate. Availability of a threshold rainfall of > 50 mm within a wide temperature range (20–30 °C) seem necessary for attainment of threshold breeding GSI (> 10.5 units) in female pool barbs. As per the present rates of climatic variability observed, our study hints the following probable consequences on reproduction of Gangetic pool barbs.

4.3.1. Overall

Owing to the low rainfall threshold (> 50 mm) pool barbs require for maturation and spawning, not much impact can be expected in terms of adjustments in breeding phenology. Furthermore, a wide water temperature threshold (20–30 °C) for breeding makes it a 'lesser worry' (Sarkar et al., 2018). In nutshell, pool barbs can breed within a wide thermal regime following slightest of rainfall events. Collating this conclusion with the present rate of climatic variability along studied stretches of River Ganga, we infer negligible threat of changing climate on reproduction of *P. sophore* in near future. Similar conclusion has been drawn for spotted snakeheads *Channa punctata* in Gangetic floodplain wetlands of West Bengal (Karnatak et al., 2018). High inter-annual variability of rainfall exists in India. Years with low rainfall is eventually offset to some extent with years of surplus rainfall (Kumar and Jain, 2011, Paul and Birthal, 2015). We suspect this trend to be manifested on the recruitment patterns of Gangetic pool barbs as well. Thus, any long-term or permanent impact of climatic variability may be subtle or non-existent. Such examples can be found in Myers et al. (2017).

4.3.2. Lower stretch

Region specific variations in breeding phenology (if any) may be caused by spatial trends of changing seasonal rainfall patterns. For example – at the lower stretch (Triveni-Farakka), the delayed offset of breeding (presently, September) in comparison to what reported earlier (August; Mitra et al. (2005)) might be due to availability of threshold

rainfall up to September. Decreasing trends of both pre- and post-monsoonal rainfall have been observed at the lower stretch. In extreme cases, the breeding phenology may be narrowed down; both onset and offset getting abnormally truncated. A similar phenomenon was recently reported for endangered Golden mahseer *Tor putitora* from lesser Himalayan region (Joshi et al., 2018).

4.3.3. Middle stretch

The present advancement of breeding onset (May) in comparison to earlier scenario (July; Srivastava (2003)) may be due to satisfaction of threshold rainfall requirement during May. Seeing the decreasing monsoonal rainfall, we suspect in extreme cases, the monsoon phase of breeding becoming shorter and recessive. Simultaneously the increment in non-monsoonal (pre-, post-monsoon) rainfall may push post-monsoonal 'minor-burst' in GSI (observed) to become dominant under extreme cases – shifting the breeding season. Similar occurrences are reported in some temperate fishes in response to changing flow pulse manifested from altered precipitation (Lynch et al., 2016, Myers et al., 2017).

4.4. Pre-spawning fitness and climate preferendum

The relationship between condition factor and reproduction has been explained in detail in Sarkar et al. (2017). $K_{spawn50}$ have been previously quantified in some catfishes (*Mystus tengara*, *M. cavasius* and *Eutropiichthys vacha*) and croaker (*Johnius coitor*) from River Ganga (Sarkar et al., 2017, 2018). No previous record of $K_{spawn50}$ exists for *P. sophore*. Several authors, as part of length-weight relationship studies, have reported a general range of Fulton's condition factor for the species (Hossain et al., 2013; Rahman et al., 2012; Sarkar et al., 2013). The present estimate of $K_{spawn50}$ falls well within the range of Fulton's condition factor given for the species *viz.* Bangladeshi Rivers (0.91–3.62 units), Bangladeshi floodplains (0.69–2.35 units) and Indian rivers (0.7–2.2 units). These observations validate our present estimate of $K_{spawn50}$ (1.59–1.67 units, median 1.63 units) which lies at a higher side of the published range(s) due to improved fitness levels of mature-ripe individuals. A detailed background of pre-spawning fitness, its relationship with climate change and evolutionary implications can be found in Sarkar et al. (2017). In the present study, dependence on rainfall for the attainment of requisite $K_{spawn50}$ was more prominent than water temperature. In fact, we tag rainfall as the primary driver during the preparatory phase of breeding in this species. Similar arguments are given in Karnatak et al. (2018) and Hossain et al. (2006) for snakehead *Channa punctata* and catfish *M. vittatus* respectively; seasonality of the flooding cycle (rainfall) rules the species' reproductive cycle. Presence of two distinct precipitation preferenda (50–150 mm and 400–700 mm) reflects the 'flexibility' of the species to attain required pre-spawning fitness both at low-mild and high rainfall conditions. Similar ability has been reported in a Riverine schebelid catfish *E. vacha* (Sarkar et al., 2017). Contrary to the concerns expressed in Naskar et al. (2017) on SIFs in general, we infer minimum impact of changing precipitation pattern (along Ganga River basin) on the preparatory phases of reproduction. Similar inference has been drawn in Karnatak et al. (2018). Likewise, in terms of thermal preferendum, a less prominent but broad thermal window (15–35 °C) exists for attainment of $K_{spawn50}$.

In the presence of such a 'flexible' climate preferendum (overall) for maintenance of requisite pre-spawning fitness, changing climatic patterns along River Ganga do not pose a high risk to the natural breeding processes of pool barbs. In reality – the quantified precipitation (50–700 mm) and thermal preferendum (15–35 °C) reflects a climate that is most likely to be available for major parts of the year. As a result, pool barbs can maintain 'near' spawning or pre-spawning fitness through major parts of the year. During this time, mere availability of breeding cue(s) may straightway induce successful spawning decisions. Owing to this 'easiness' in attainment of requisite $K_{spawn50}$ under

prevailing conditions, the chances of 'skipped spawning' decisions in pool barbs facing climatic variability also seem minimum (Jorgensen et al., 2006).

4.5. Size at maturity

The first maturity of female *P. sophore* encountered in the present study (4.7 cm) matches with some earlier observations (female), but only for waters outside Indian territory. Ahamed et al. (2015), Halls (2005), Hossain et al. (2012) and Tareque et al. (2009) recorded 4.2–5.2 cm as length at first maturity; deviating only ± 0.5 cm from the present estimate. Interestingly, all the records from Indian waters are higher than the first maturity we encountered. Mitra et al. (2005) reported 6.1–6.5 as size at first maturity from Gangetic floodplains of West Bengal. Reddy and Rao (1992) reported 9 cm from Hussain Sagar lake in Hyderabad. Kiran (2015) documented 7–8 cm from a small irrigation tank (reservoir) in Karnataka from samples collected during 2006. To the best of our knowledge, these are the only historical records available (1992–2006) from Indian waters for a preliminary comparison. If these records are compared with, a reduction in size at maturity of female pool barbs appear plausible. We encountered the smallest mature female (4.7 cm) from the posterior lower stretch of River Ganga (Triveni) which is about 1.4–1.8 cm shorter than estimates of Mitra et al. (2005) from same region, almost a decade ago. This further reinforces our hypothesis surrounding a probable reduction in size at maturity as a response to changing climate – subject to future validation. Changes (reduction in most cases) in sizes at maturity have already been listed among major reproductive adaptation in fishes to changing climate (Myers et al., 2017; Lynch et al., 2016; Whitney et al., 2016).

The size at 50% maturity (L_{M50}) estimated was found to be higher (8.8 ± 0.2 cm) than the first maturity estimate (4.7 cm). This difference also signifies the importance of studying 'first maturity' and 'size at 50% maturity' (*often termed as*, size at first maturity) as 'separate' entities; not synonymous as perceived in many traditional studies (Gupta, 2015, Ainsley et al., 2011). The differences in sizes at maturity may be attributed to multiple reasons – (a) difference in sample composition or distribution, (b) increasing proportion of smaller-sized mature females due to earlier spawning, fishing pressure or any other climato-limnological influence (researchable issue), (c) difference in methods of estimation (Sarkar et al., 2018). Therefore, reporting data on both the abovementioned parameters under 'sizes of maturity' may be more appropriate and insightful for future researchers or conservation biologists.

4.6. Future directions

Our present attempt might have been limited by some practical difficulties and inherent complex nature of the experiment itself (discussed above). The future studies may attempt to validate the present observations, estimates and hypotheses from similar and extended regions. In addition to validating information for this species, the species selection needs to be expanded – subject to the availability of historical record(s) on reproduction and breeding parameters. This will simultaneously validate the proposed framework of assessment. Conclusions drawn from such 'repeated' attempts might be more accurate and representative for reproductive adaptation of minnows under changing climatic environment. Although we did not encounter any noticeable inter-annual variability in breeding behaviour of Gangetic pool barbs within our studied area, we recommend systematic ground-studies to be at least for two years or longer. A longer duration of experiment (ideally, 4–5 years) might be necessary when noticeable inter-annual variability in breeding behaviour is exhibited by a species, that too within the studied area. Additionally, for authentic modelling purposes, the dataset should resemble (as closely as possible) the distribution in natural population to eliminate any biasedness in the predictions.

Therefore, a random, frequent and heterogenous sample composition should be prioritized. The present estimates may also be re-calculated in future attempts using different statistical tools (or methods) to detect reliability.

5. Conclusion

Information on climato-hydrological influences on breeding of a Gangetic minnow *P. sophore* (pool barbs) was generated for the first time in relation to climatic variability, employing an alternative approach. It was found that changes in rainfall pattern may have the most profound effect on gonad maturation and spawning in fish followed by the effect warming climate. In nutshell, pool barbs can breed within a wide thermal regime following slightest of rainfall events. Collating this conclusion with the present rate of climatic variability along studied stretches of River Ganga, we infer 'negligible threat' of changing climate on reproduction of *P. sophore* in near future. Owing to the 'easiness' in attainment of requisite K $_{spawn50}$ under prevailing conditions, the chances of 'skipped spawning' decisions in pool barbs facing climatic variability also seem minimum. These are in contrary to the presumptions which anticipate otherwise. A 'probable' two-month advancement-cum-extension of breeding phenology in the middle stretch of River Ganga was revealed. Suspicions on the possibility of a shifted and/or extended breeding phenology at the lower stretches were also raised. In terms of size at maturity, an apparent reduction was observed. Future studies may attempt to validate the present observations, estimates and hypotheses from similar and extended regions, which will also validate the proposed framework.

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Declaration

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Conflict of Interest

The authors declare that they have no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.03.037.

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